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INTRODUCTION: REVIEW

Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds

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ABSTRACT: Technological advances in recent years have seen an explosion of tracking and stable isotope studies of seabirds, often involving repeated measures from the same individuals. This wealth of new information has allowed the examination of the extensive variation among and within individuals in foraging and migration strategies (movements, habitat use, feeding behaviour, trophic status, etc.) in unprecedented detail. Variation is underpinned by key life-history or state variables such as sex, age, breeding stage and residual differences among individuals (termed 'individual specialization'). This variation has major implications for our understanding of seabird ecology, because it affects the use of resources, level of intra-specific competition and niche partitioning. In addition, it determines the responses of individuals and populations to the environment and the susceptibility to major anthropogenic threats. Here we review the effects of season (breeding vs. nonbreeding periods), breeding stage, breeding status, age, sex and individual specialization on foraging and migration strategies, as well as the consequences for population dynamics and conservation.

KEY WORDS: Individual specialization · Consistency · Sexual segregation · Age effects · Central-place constraint · Intrinsic variation · State dependence · Life-history

INTRODUCTION

The burgeoning of tracking and stable isotope studies of seabirds and other marine predators since the 1990s has provided a wealth of information on numerous aspects of their ecology and life-history, including the striking variation in movement patterns and foraging behaviour of individuals (Phillips et al. 2008, Wakefield et al. 2009a). Until relatively recently, this variation was examined largely by testing for effects of factors such as species, colony, sex, age, year, season (breeding vs. nonbreeding period), breeding phase or breeding status. Much less attention was paid to the residual variation among individuals after accounting for these group effects. This residual variation was considered to define 'individual specialization' in the seminal review by Bolnick et al. (2003) and is also the focus of research on 'behavioural syndromes' or 'animal personalities' in the field of animal behaviour (Dall et al. 2012). Research on individual variation has burgeoned in the last decade, spurred partly by reductions in cost and mass of tracking devices, allowing larger sample sizes, and by the increasing use of more powerful statistical techniques (Carneiro et al. 2017, this Theme Section).

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Most seabirds show striking changes in distribution associated with stage of the annual cycle. Many species are migratory, making directed movements from breeding to nonbreeding grounds to exploit seasonal peaks in prey abundance or to avoid inclement weather, with implications for survival and subsequent fecundity (Daunt et al. 2014, Reiertsen et al. 2014). The changing degree of central-place constraint during the breeding period — from pre-laying through incubation, brood-guard and later chick-rearing (post-guard) — can lead to major shifts in distribution, activity patterns or diet within individuals (Hedd et al. 2014, Quillfeldt et al. 2014). There may be within-breeding-season (date-related) differences in distribution or diet, which reflect extrinsic changes in the environment (Phillips et al. 2009b). In addition, some seabirds (particularly albatrosses and petrels) adopt a bimodal (or dual) foraging strategy during chick-rearing, in which adults alternate between foraging close to the colony and increasing feeding frequency for the benefit of the chick, and foraging further afield to recover their own body condition (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994).

There is mounting evidence that movements and distributions of seabirds are influenced by age and breeding status. Failed breeders often depart on their migration sooner than successful ones (Phillips et al. 2005, Bogdanova et al. 2011, Hedd et al. 2012), and they may spend the late breeding season in the same areas as deferring (sabbatical) breeders, but be partially or completely segregated from active breeders (Phillips et al. 2005, González-Solís et al. 2007, Reid et al. 2014). In this way, nonbreeders (failed or deferring) may be avoiding competition with breeders (Clay et al. 2016). Juvenile and immature seabirds avoid competition with adults — possibly to compensate for poorer foraging skills — by using less productive habitats and increasing their foraging time (Daunt et al. 2007b, Fayet et al. 2015). Their distributions frequently differ from those of adults, often markedly so during the nonbreeding period even though adults are no longer limited by the central-place foraging constraint (but see Péron & Grémillet 2013, Gutowsky et al. 2014, de Grissac et al. 2016).

Age effects on foraging ability are often apparent amongst breeders: younger or less experienced birds may forage less efficiently, with implications for breeding success (Daunt et al. 2007b, Limmer & Becker 2009, Harris et al. 2014a, Le Vaillant et al. 2016), or feed at lower trophic levels (Le Vaillant et al. 2013). Inferior foraging success among younger individuals is thought to reflect the poorer skills in identifying or catching prey or in selecting suitable locations, weaker motor control or physiological fitness (e.g. cardiovascular or muscular performance) of young birds or the selective disappearance of poor phenotypes among the adult population. Although there is evidence that foraging ability can decline in old age (Catry et al. 2006), changes in behaviour may not be detectable — despite physiological ageing (Elliott et al. 2015) — or are apparent only in particular environments (Lecomte et al. 2010, Froy et al. 2015). Moreover, differences between old and young animals can be difficult to interpret, because lower activity (e.g. more time on the water recorded by a leg-mounted immersion logger) might indicate either inferior physiological function or greater efficiency allowing more discretionary time to be spent resting (Catry et al. 2011).

Sexual segregation and other between-sex differences in foraging behaviour are apparent in many seabirds. This may reflect habitat specialization or avoidance of competition in sexually dimorphic species and sex role specialization or sex-specific nutrient requirements in monomorphic or dimorphic species (Lewis et al. 2002, Phillips et al. 2004, 2011). Sex differences in distribution and behaviour of seabirds tend to be more apparent during particular periods, for example during pre-laying (presumably related to sex-role partitioning of nest defense), affecting attendance patterns (Hedd et al. 2014, Quillfeldt et al. 2014). However, such effects are far from universal; despite a degree of spatial segregation, activity patterns of male and female albatrosses are comparable during the breeding and nonbreeding periods, suggesting little difference in prey type or foraging method (Mackley et al. 2011, Phalan et al. 2007). Similarly, in the 2 recent studies that recorded sex differences in the proportions of residents and migrants, the effects were in opposite directions (Pérez et al. 2014, Weimerskirch et al. 2015).

Variation among and within individuals in foraging distribution and behaviour has major implications for our understanding of seabird ecology because it affects the use of resources, level of intra-specific competition and niche partitioning (Phillips et al. 2004, de Grissac et al. 2016). In addition, it determines the responses of individuals and populations to environmental drivers (including climatic change) and the overlap with, and hence susceptibility to major anthropogenic threats, including fisheries and pollutants (Phillips et al. 2009a, Granadeiro et al. 2014, Patrick et al. 2015). Individual variation is also at the root of carry-over effects, whereby processes in one season have consequences in subsequent sea-

sons (Harrison et al. 2011). Surprisingly, however, there are rarely demonstrable life-history consequences of individual consistency in foraging strategies *per se* despite the many studies of adult quality (consistent individual differences in breeding performance) in seabirds (Lescroël et al. 2009, Crossin et al. 2014, but see Patrick & Weimerskirch 2017).

Here we review the intrinsic group effects underlying individual variation in foraging and migration patterns of seabirds, including breeding stage, season (breeding vs. nonbreeding period), breeding status, age, sex and—after those have been accounted for—the incidence, causes and consequences of the individual effects that remain. We consider these last, residual effects to be synonymous with individual specialization sensu Bolnick et al. (2003) and expect specialists to show repeatability or consistency in foraging distribution, behaviour or diet. We do not review effects of colony, as these may reflect differences in resource availability or habitat accessibility, nor effects of date or year *per se*, as these reflect environmental variation and are extrinsic to individual decisions and trade-offs. We explore whether the degree of variation among and within individuals (i.e. both groups effects and specialization) depends on phylogeny, biogeography or other factors and focus on the consequences for life-histories and population dynamics and the implications for seabird conservation. The impetus for this review and for this Theme Section on 'Individual variability in seabird foraging and migration' in *Marine Ecology Progress Series* was the session on 'Individual variation in movement strategies' at the 2nd World Seabird Conference in Cape Town, South Africa, 27–30 October, 2015.

EFFECTS OF THE ANNUAL CYCLE

Breeding stage and season (breeding vs. nonbreeding period)

Changes in seabird diet across the annual cycle, particularly over different stages of the breeding period, have been studied for several decades (Barrett et al. 2007), but until the advent of suitable tracking technologies, information on year-round foraging behaviour of seabirds was scarce. Subsequently, many studies have recorded foraging distribution and behaviour of individuals over extended periods, showing that these vary markedly throughout the annual cycle; some of these changes reflect differences in food availability or the underlying biophysical environment, and others are directly related to changes in reproductive demands and central-place foraging (Phillips et al. 2008, González-Solís & Shaffer 2009). Energy requirements and breeding duties change across the annual cycle, limiting foraging in time and space (including to the most productive habitats) to different extents.

During pre-laying, birds visit the colony frequently or remain there for a prolonged period for pair bonding and nest defence, but they are still free from parental duties and may have time available for long trips. Although the constraints for males and females may differ, individuals typically forage further from the colony and in more productive waters than in later stages (Phillips et al. 2006, Paiva et al. 2008, Pinet et al. 2012, Hedd et al. 2014). During incubation, most seabirds alternate incubation bouts, with one parent incubating the clutch while the other is at sea. In penguins, albatrosses, petrels and alcids, birds may fast for several weeks on the nest while the partner engages in foraging trips that are longer and further afield than during chick rearing (Hull 2000, Phalan et al. 2007, Ito et al. 2010, Péron et al. 2010, Hedd et al. 2014). Nevertheless, trips usually shorten when hatching approaches, allowing the chick to be fed within a few days (Weimerskirch et al. 1997, González-Solís 2004). In gulls and skuas, however, incubation bouts are relatively short, and the foraging range during that phase can be similar or shorter than during chick rearing (Carneiro et al. 2014, Camphuysen et al. 2015).

During brooding, the parents alternate foraging with guarding the chicks, which are rarely left unattended in order to reduce exposure to the elements or predators. In pelagic seabirds, this is often regarded as the period with the greatest energy requirements, since an adult must forage both to meet its own demands during the subsequent brooding stint and those of the chicks (Ricklefs 1983). In some species (including albatrosses, petrels and penguins), parents are forced to forage closer to the colony than in any other stage (Hull 2000, Charrassin & Bost 2001, Phillips et al. 2004, González-Solís et al. 2007), even though the areas visited may not be optimal, leading to progressive deterioration in parental body condition (Weimerskirch & Lys 2000, Green et al. 2009). In addition, the requirements of the chick in terms of prey energetic or nutritional content, size or digestibility may necessitate a change in foraging behaviour of the adult (Davoren & Burger 1999, Isaksson et al. 2016). Several studies have shown that parents feed their chicks with a high-quality diet, for example selecting lipid-rich fishes (Wilson et al. 2004, McLeay et al. 2009, Bugge et al. 2011, Dänhardt et al. 2011), and a

failure to do so may reduce chick survival (Annett & Pierotti 1999, Grémillet et al. 2008). Alternatively, selection of high quality prey may reflect the need to maximise net energy gain per unit foraging effort for parents that are unable to carry more than one item in their bill (Wilson et al. 2004). In species delivering mainly undigested food, chicks are limited in terms of the size of prey they can swallow, and parents are typically forced to seek small items, steadily increasing the size with chick age, which may require parents to change prey types and foraging areas over the chick-rearing period (Pedrocchi et al. 1996, Rodway & Montevecchi 1996, McLeay et al. 2009).

In many species there is a post-brooding period (crèche in penguins) when parents leave chicks unattended except when delivering meals so that they can increase trip length. Initially, the foraging range usually remains more constrained than during incubation (Phillips et al. 2004, Saraux et al. 2011, Froy et al. 2015), presumably because chicks have a lower fasting capability than incubating adults until the mid- to late chick-rearing phase (Phillips & Hamer 1999). Trip duration tends to increase and parents forage further away from the colony as the chick-rearing period progresses (Weimerskirch & Lys 2000, Dall'Antonia et al. 2001, Rishworth et al. 2014b). These longer trips are likely prompted by the chicks' increased fasting capability and energetic demand, as well as a deterioration in food availability or an increase in foraging conspecifics enhancing density-dependent competition near the colony (Rishworth et al. 2014b). The ability to increase intervals between feeding is limited by the maximum payload, which is inversely related to adult body mass in Procellariiformes (Phillips & Hamer 2000). Food delivery rates also depend on whether the adults forage in coastal or inshore waters and deliver food that is fresh and carried in the bill (terns and alcids), partially-digested in the stomach (gulls, penguins and other taxa) or further digested to an energy-dense stomach oil in the proventriculus (Procellariiformes; except diving petrels, Pelecanoididae); in this last group, the single chick stores extensive fat reserves, allowing the adults to exploit more remote areas (Ricklefs 1983, Phillips & Hamer 1999). Changes in trip duration during breeding can be detected using stable isotopes, and an increase in foraging range may be associated with an expansion of the isotopic niche (Ceia et al. 2014).

For breeding, seabirds need land that is free of terrestrial predators. Such breeding grounds may be distant from productive foraging sites. One mechanism for coping with low food availability close to the breeding colony is to adopt a so-called 'dual foraging' strategy, when parents alternate between short and long foraging trips to balance their own energetic requirement with that of the chick (Chaurand & Weimerskirch 1994, Weimerskirch et al. 1994). During these short trips, parents forage within shorter distances, maximising provisioning rates; however, this apparently reduces their body condition, causing the adult to switch to more distant and more productive waters with predictable food resources (frontal zones, neritic areas, etc.) to restore its own reserves. The dual foraging strategy is seen in many albatrosses, shearwaters and other petrels, but there is a great deal of variability among species and populations, potentially related to differences in foraging strategies and resource distribution around colonies or between years (Granadeiro et al. 1998, Baduini & Hyrenbach 2003, Phillips et al. 2009b). A similar but less flexible strategy has also been postulated for penguins (Ropert-Coudert et al. 2004, Saraux et al. 2011). Dual foraging has also been described in auks (Welcker et al. 2009), possibly because the energetic cost of transit in this group is particularly high (Costa 1991, Thaxter et al. 2010).

Changes in foraging behaviour also occur in the nonbreeding period. After breeding, most species of seabirds migrate to more suitable habitats, avoiding low temperatures, shorter days and reduced food availability around colonies. In some populations, individuals move to a post-breeding, stopover area, presumably offering good foraging opportunities at that time of year, where they may spend considerable time before departing for their main wintering grounds (Anker-Nilssen & Aarvak 2009, Frederiksen et al. 2012, Bogdanova et al. 2017, this Theme Section). Both conventional diet (stomach content analysis) and stable isotope studies indicate that wintering seabirds can change their diet or widen their trophic niche, since individuals are no longer central-place foragers and are free to select their favoured habitat or prey (Cherel et al. 2007, Karnovsky et al. 2008, Hedd et al. 2010, Harris et al. 2015). It is important to note that we lack knowledge for most seabirds of their prey during the winter; although stable isotope studies offer a partial solution, ideally these need to control for changes in isotopic baselines because of the scale of seabird movements (Meier et al. 2017).

Activity levels decrease during part of or the entire nonbreeding period in Procellariiformes (Mackley et al. 2011, 2010, Cherel et al. 2016), sulids (Garthe et al. 2012), skuas (Magnusdottir et al. 2014, Carneiro et al. 2016) and alcids (Mosbech et al. 2012). Reasons for this decrease may include lower energetic demands, freedom from parental care duties and removal of the

central-place foraging constraint, higher food availability or lower costs of thermoregulation. In addition, productive nonbreeding grounds may allow for a sit-and-wait foraging strategy that is more energy-efficient, or food availability may be enhanced by the activities of subsurface predators or fisheries (Péron et al. 2010). Seabirds generally, but not always, moult in the nonbreeding period to avoid overlap with other energetically demanding processes, such as reproduction or migration (Bridge 2006, Catry et al. 2013b). This may result in flight impairment, which would explain a decrease in activity levels in the winter in some species (Cherel et al. 2016), or in flightlessness, which may drive movements (particularly by auks) to specific moulting areas (Linnebjerg et al. 2013, Frederiksen et al. 2016).

Lower activity during the nonbreeding period is far from universal, and species that breed in high latitudes, are resident year-round, or have limited capacity to migrate, cope with winter conditions by increasing their activity levels. Indeed, foraging time of cormorants or shags breeding at high latitudes peaks in mid- to late winter, possibly due to reduced prey availability or high energetic costs associated with thermoregulation (Grémillet et al. 2005, Daunt et al. 2006, Lewis et al. 2015), and penguins sometimes dive longer and deeper to exploit less accessible prey during winter (Moore et al. 1999, Charrassin & Bost 2001, Green et al. 2005).

Breeding status

Studies of seabird foraging and movements during the breeding season usually focus on breeding adults because of the relative ease with which they can be caught for logger deployment and retrieval. However, an important component of the breeding population comprises individuals that are not breeding or have failed in their breeding attempt, and an increasing number of studies aim to quantify the foraging dynamics of these groups and to test whether they show different behaviours compared to breeding adults. Much of the attention has been directed at failed breeders, whose failure may have been natural, a consequence of the deployment, or induced as part of a manipulative experiment (Phillips et al. 2005, Bogdanova et al. 2011, Ponchon et al. 2014, 2015). Failed breeders often continue to associate with the colony, operating as central-place foragers but expanding their foraging areas (González-Solís et al. 2007). The spatial overlap with breeders varies among populations; it can be high (Ponchon et al. 2014), moderate (Phillips et al. 2008), or there may be marked segregation (Jaeger et al. 2014, Reid et al. 2014, Clay et al. 2016). Further, failed breeders may make visits to other colonies when breeders are still actively rearing chicks; this behaviour is interpreted as prospecting potential new breeding sites and may be motivated by having failed at the current location (Fijn et al. 2014, Ponchon et al. 2014, 2015). In contrast, successful breeders do not undertake prospecting trips or only do so after breeding is finished (Fijn et al. 2014, Ponchon et al. 2014, 2015).

Quantifying differences in foraging and movements between breeding and nonbreeding individuals (the latter including deferring breeders and older pre-breeders, but not failed breeders) during the breeding season is hampered by the difficulty in capturing nonbreeders to deploy data loggers. There is considerable indirect evidence from observations at breeding sites that nonbreeders often attend the colony in the breeding season and act as central-place foragers, suggesting that foraging overlap with breeders would be substantial (Aebischer 1986, Harris & Wanless 1997). This has been confirmed by tracking black-browed albatross *Thalassarche melanophris* at South Georgia (Phillips et al. 2005), but in the same species elsewhere and in Cory's shearwater *Calonectris borealis*, deferring adults segregate isotopically from breeders, indicating differences in their foraging niche (Campioni et al. 2015). Some of the most compelling evidence for spatial segregation based on breeding status during the breeding season is for biennial breeders such as the wandering albatross *Diomedea exulans* and grey-headed albatross *Thalassarche chrysostoma*, in which a proportion of individuals spend the sabbatical period entirely at sea, thousands of kilometres from the colony (Weimerskirch et al. 2015, Clay et al. 2016).

At the end of the breeding season, timing of departure from breeding colonies is strongly dependent on breeding status, with failed and deferred breeders typically leaving significantly earlier than successful breeders (Phillips et al. 2005, 2007, Bogdanova et al. 2011, Hedd et al. 2012, Catry et al. 2013a). Carry-over effects of breeding status on migration may persist into the nonbreeding period, with evidence that failed breeders arrive at wintering grounds early and depart the wintering grounds later or earlier, depending on the study species (Phillips et al. 2005, Catry et al. 2013a, Bogdanova et al. 2017). There may also be differences in migration destination; in black-legged kittiwakes *Rissa tridactyla*, failed breeders wintered further from the breeding colony on average than successful breeders (Bogdanova et al.

2011), and evidence from stable isotope analyses suggested that failed wandering albatrosses differed from successful and deferred breeders in terms of distribution in the following winter (Jaeger et al. 2014). Such differences are not always apparent, however, and high overlap of individuals of differing breeding status during the winter has been observed in other studies (Phillips et al. 2005, 2007, Hedd et al. 2012, Clay et al. 2016).

EFFECTS OF AGE

Age-specific foraging and movements

Comparisons of juveniles and adults

A long-standing theory in avian ecology is that juveniles have reduced survival probability because they have a lower foraging proficiency, resulting from a lack of experience or physical ability; this theory is supported by widespread empirical evidence across many avian species (Marchetti & Price 1989, Wunderle 1991). These are topics of particular interest in seabirds because of their slow maturity, which suggests that the development of foraging is complex and requires an extended period of learning. A list of studies that tested for differences in foraging and migration between juveniles, immatures and adult seabirds is provided in Table 1. Early work on seabirds, based primarily on visual observations of feeding individuals or flocks, provided clear evidence that juveniles had lower foraging success than adults (Orians 1969, Dunn 1972, Burger & Gochfeld 1981, Porter & Sealy 1982, Greig et al. 1983, MacLean 1986). Comparisons of multiple age classes showed progressive improvement in performance in the prebreeding years (Orians 1969, Porter & Sealy 1982, MacLean 1986), and more recent studies indicate that foraging effort and skills develop rapidly after fledging (Yoda et al. 2004, Daunt et al. 2007b, Guo et al. 2010, Orgeret et al. 2016); however, the foraging proficiency of juveniles throughout their first winter remains lower than that of adults, linked to a lower survival probability (Daunt et al. 2007b, Orgeret et al. 2016). Indeed, in terms of survival prospects, the critical period is around independence, which, depending on the species, may occur at fledging or be a gradual process as parents progressively reduce post-fledging provisioning rate (Daunt et al. 2007b, Riotte-Lambert & Weimerskirch 2013, Orgeret et al. 2016).

Biologging and biotelemetry have been instrumental in the study of movements during the juvenile phase (Table 1). It has long been apparent from ringing recoveries that juvenile seabirds often disperse long distances and generally have a wider distribution than adults (Weimerskirch et al. 1985), but attachment of loggers to chicks has enabled the critical months after fledging to be investigated in detail. Fledglings typically undertake rapid and large-scale movements in the first few months and (in flying seabirds) appear to target favourable wind patterns, sometimes delaying departure until these become available (Kooyman et al. 1996, Åkesson & Weimerskirch 2005, Trebilco et al. 2008, Alderman et al. 2010, Riotte-Lambert & Weimerskirch 2013, Blanco et al. 2015, de Grissac et al. 2016, Weimerskirch et al. 2016). Such movements can lead to striking segregation from adults in the nonbreeding period (Kooyman et al. 1996, Jorge et al. 2011, Riotte-Lambert & Weimerskirch 2013). However, this is not universal, and the degree of segregation seems largely to stem from among-species variation in adult movements, with the greatest segregation in species where adults stay close to colonies throughout the year (Grémillet et al. 2015, de Grissac et al. 2016). Juveniles often forage in less productive waters than adults, which may be key to explaining their lower survival probability (Thiebot et al. 2013, Gutowsky et al. 2014, Jaeger et al. 2014).

Detailed analyses suggest that it may take juveniles several months to attain the flight ability of adults (Riotte-Lambert & Weimerskirch 2013). In association with this, the structure of their movements also differs markedly from adults, with evidence of longer, more sinuous pathways in juveniles (Péron & Grémillet 2013, Riotte-Lambert & Weimerskirch 2013, Missagia et al. 2015, de Grissac et al. 2016). There is considerable interest in how individuals are able to navigate during this juvenile period (Guilford et al. 2011, Fayet et al. 2015, de Grissac et al. 2016). However, understanding the mechanisms is challenging because of the lack of information on potential cues (ocean features, presence of conspecifics, etc.), but detailed analyses of movements suggest extensive variation among species in the relative importance of inheritance, cultural mechanisms and acquired memory through exploration (Guilford et al. 2011, Péron & Grémillet 2013, de Grissac et al. 2016).

The immaturity period between the juvenile (first winter) phase and adulthood is also a challenge to study. Device deployments are restricted to the few species where immatures can be captured (generally at colonies), as loggers and transmitters deployed on feathers on the last occasion when these birds were accessible on land (at or before fledging) remain secure only until the first moult, and those attached

Table 1. Studies testing for differences in foraging and migration among juveniles (first year, J), immatures (subsequent sub-adult age classes, I) and adult seabirds (A). Ix = inexperienced; Ex = experienced; Y = yes (effect detected); N = no effect

Taxon	Age classes[a]	Nonbreeding season location	Breeding season location	Foraging effort	Foraging success	Dive characteristics	Flight characteristics	Reference
Charadriiformes								
Herring gull *Larus argentatus*	I, A				Y			Greig et al. (1985)
	J, I, A				Y			MacLean (1986)
Lesser black-backed gull *Larus fuscus*	J, I, A	Y	Y					Jorge et al. (2011)
Bonaparte's gull *Chroicocephalus philadelphia*	J, I, A				Y			MacLean (1986)
Ring-billed gull *Larus delawarensis*	J, I, A				Y			MacLean (1986)
Gull species (*Larus* spp.) × 4	J, I, A				Y			Burger & Gochfeld (1981)
Gull spp. × 6	J, I, A				Y			Porter & Sealy (1982)
Auk spp. × 2	J, I, A				Y			Porter & Sealy (1982)
Sandwich tern *Thalasseus sandvicensis*	J, older				Y			Dunn (1972)
Pelecaniformes								
Brown pelican *Pelecanus occidentalis*	J, A[b]				Y			Orians (1969)
Northern gannet *Morus bassanus*	I, A		Y					Votier et al. (2011)
	J, A	N						Grémillet et al. (2015)
Brown booby *Sula leucogaster*	J			Y			Y	Yoda et al. (2004)
Red-footed booby *Sula sula*	J			Y				Guo et al. (2010)
European shag *Phalacrocorax aristotelis*	J, A			Y				Daunt et al. (2007b)
Procellariiformes								
Wandering albatross *Diomedea exulans*	J	Y					Y	Åkesson & Weimerskirch (2005)
	J, I	Y					Y	Weimerskirch et al. (2006)
	J, I, A	Y		Y			Y	Riotte-Lambert & Weimerskirch (2013)
	I, A	Y	Y					Jaeger et al. (2014)
Shy albatross *Thalassarche cauta*	J	Y						Alderman et al. (2010)
Black-footed albatross *Phoebastria nigripes*	J, A	Y						Gutowsky et al. (2014)
Black-browed albatross *Thalassarche melanophris*	I, A	Y					Y	Petersen et al. (2008)
White-capped albatross *Thalassarche steadi*	I, A	Y					Y	Petersen et al. (2008)
Black-browed albatross *Thalassarche melanophris*	I, A	Y						Campioni et al. (2015)
Northern giant petrel *Macronectes halli*	J, A	Y						Trebilco et al. (2008)
Southern giant petrel *Macronectes giganteus*	J, A	Y					Y	Blanco et al. (2015)
	J, A	Y						Trebilco et al. (2008)
Cory's shearwater *Calonectris borealis*	I, A	Y						Campioni et al. (2015)
	Ix, Ex	Y		Y				Missagia et al. (2015)
Manx shearwater *Puffinus puffinus*	I, A		N		Y			Fayet et al. (2015)
Scopoli's shearwater *Calonectris diomedea*	J, A	N						Grémillet et al. (2015)
	J, I, A	N		Y			Y	Péron & Grémillet (2013)
Sooty shearwater species	J, I, A				Y			Porter & Sealy (1982)
Procellariiformes spp. × 9	J, A	Y/N					Y	de Grissac et al. (2016)
Sphenisciformes								
Emperor penguin *Aptenodytes forsteri*	J	Y						Kooyman et al. (1996)
	J	Y						Thiebot et al. (2013)
King penguin *Aptenodytes patagonicus*	J, A					Y		Orgeret et al. (2016)

[a]Studies restricted to juveniles typically compare with adults based on past work/unpublished data. [b]First winter birds defined as immatures

to leg rings require the individual to be recaptured after return to the colony (Daunt et al. 2007b, de Grissac et al. 2016). Tracking has demonstrated that immatures show limited or no segregation from adults during the nonbreeding season until the point when adults return to colonies in preparation for breeding (Petersen et al. 2008, Péron & Grémillet 2013). Older immatures may also associate with colonies and operate as central-place foragers, although trip structure, trip duration and resource use differ from those of breeding adults (Votier et al. 2011, Riotte-Lambert & Weimerskirch 2013, Campioni et al. 2015). However, immatures also undertake prospecting movements, where they visit multiple colonies either during the breeding season or autumn migration, resulting in seasonal segregation from breeding adults from the same site (Votier et al. 2011, Péron & Grémillet 2013). In addition to these spatial differences associated with key age-specific behaviours, immatures exhibit lower foraging efficiency than adults (Fayet et al. 2015), supporting the theory that the acquisition of foraging skills is a lengthy and complex process in seabirds that may in part explain the long immaturity phase.

Adults

An increase in reproductive success with age is widespread among iteroparous breeders (Clutton-Brock 1988, Newton 1989, Forslund & Pärt 1995). One of the principal mechanisms underpinning this pattern is an improvement in foraging performance with age (Curio 1983). Seabirds show marked changes in foraging performance in early life, and for some species, the immature period may be sufficiently long that individuals have reached full foraging capability by the time they recruit into the breeding population (Weimerskirch et al. 2005). Alternatively, individuals may require additional skills or experience to forage successfully both for themselves and their young (Haug et al. 2015).

Despite growing evidence of differences in foraging performance between young and older breeders (Table 2), there have been few definitive studies of the underpinning mechanisms. Young breeders may be less successful at foraging because they are poorer at locating prey, physically less capable (Curio 1983) or because they are showing restraint because of their higher residual reproductive value (Williams 1966). A further challenge is to establish whether individuals improve their foraging performance with age, and if the higher average performance of older age classes is due to differential survival rates of individuals of differing foraging abilities (Smith 1981, Nol & Smith 1987, Reid et al. 2010). Longitudinal studies are therefore essential to establish the relative importance of within-individual improvements and natural selection (Limmer & Becker 2009). In addition, it has proved difficult to tease apart age from experience, since the two are closely correlated (Pärt 1995). Finally, most seabirds breed seasonally, and younger individuals usually breed later in the year and less successfully; as such, intrinsic performance is potentially confounded by a deterioration in environmental conditions later in the season, and experimental approaches are required to tease these processes apart (Daunt et al. 1999, 2007a).

Habitat use and foraging behaviour and efficiency may vary among different age classes. Although progressive changes in habitat type with age during the nonbreeding season have been detected using stable isotope analyses (Jaeger et al. 2014), in another recent study, there were no significant differences in migration destinations or strategies between adult age classes (Pérez et al. 2014). More attention has focussed on age-related foraging performance during the breeding season (Table 2). In line with theory, young breeders often obtain less food than older breeders (Daunt et al. 2007a, Limmer & Becker 2009, Le Vaillant et al. 2013), and their diet may be of lower quality (Navarro et al. 2010), with impacts on chick growth rates and reproductive success (Daunt et al. 2001, Limmer & Becker 2009). Such patterns may result from age-specific differences in foraging efficiency (Daunt et al. 2007a, Limmer & Becker 2009). Older breeders may have greater experience in locating profitable feeding areas, as shown in Cory's shearwater where site fidelity to productive areas was higher in experienced age classes (Haug et al. 2015). Older individuals may also have physical advantages; for example, Le Vaillant et al. (2012, 2013) showed that they dive deeper, experience reduced underwater drag and undertake more prey pursuits than younger breeders. Older breeders may increase foraging effort to maximise chick provisioning rates, in particular when environmental conditions are poor (Daunt et al. 2007a). Alternatively, they may reduce foraging effort, potentially to maximise time spent on other activities such as resting or guarding the young (Weimerskirch et al. 2005, Zimmer et al. 2011, Harris et al. 2014a, Lewis et al. 2015, Le Vaillant et al. 2016). Young individuals may increase foraging effort to compensate for their reduced efficiency; for example, Weimerskirch et al. (2005) showed that younger and older breeders expended similar foraging effort dur-

Table 2. Studies testing for age-specific differences in foraging and migration among adult seabirds. Age classes: young (Y), middle-aged (M), old (O). +: minimum age. Main comparison classed either as young vs. middle-aged (YM) or middle-aged vs. old (MO)

Taxon	Age classes	Ages	Main comparison	Non-breeding location	Breeding location	Timing of foraging	Foraging effort	Foraging success	Dive characteristics	Flight characteristics	Reference
Charadriiformes											
Common tern *Sterna hirundo*	Y, M	n/a[a]	YM					Y			Limmer & Becker (2009)
Audouin's gull *Larus audouinii*	Y, M	4–11	YM					Y			Navarro et al. (2010)
Brünnich's guillemot *Uria lomvia*	Y, M, O	3–30	MO						N		Elliott et al. (2015)
Pelecaniformes											
European shag	Y, M	2; >2	YM				Y	Y			Daunt et al. (2007a)
Phalacrocorax aristotelis	Y, M, O	2–3; 4–5; 6–7; 8–9; 10+	YM,MO	N							Grist et al. (2014)
	Y, M, O	2–19	YM,MO				N				Lewis et al. (2015)
Imperial shag *Phalacrocorax atriceps*	Y, M	2–3; min 6–7[b]	YM						Y	Y	Harris et al. (2014a)
Procellariiformes											
Wandering albatross	Y, M	6–11; 12–30	YM			Y	Y				Weimerskirch et al. (2005)
Diomedea exulans	Y, M, O	6–48+	MO		Y		Y				Lecomte et al. (2010)
	Y, M, O	3–11; 7–29; >29	YM, MO	Y	Y						Jaeger et al. (2014)
	Y, O	8–16; 25–37	MO		N						Froy et al. (2015)
	Y, M, O	8–35+	MO		N						Froy et al. (2015)
Grey-headed albatross *Thalassarche chrysostoma*	M, O	<28; 35+[c]	MO				Y	Y			Catry et al. (2006)
Cory's shearwater	M, O	13–20; >26	MO				Y				Catry et al. (2011)
Calonectris borealis	Y, M, O	n/a[d]	YM, MO	N							Pérez et al. (2014)
	Y, M	7–14; >20[b]	YM		Y						Haug et al. (2015)
Sphenisciformes											
King penguin	Y, M	5; 8–9	YM						Y		Le Vaillant et al. (2012)
Aptenodytes patagonicus	Y, M	5; 9	YM				Y	Y	Y		Le Vaillant et al. (2013)
	Y, M	4–11	YM				Y				Le Vaillant et al. (2016)
Little penguin *Eudyptula minor*	Y, M, O	3–4; 5–10; 11–14	YM, MO						Y		Zimmer et al. (2011)
	M, O	5–11; 12–18	MO		Y		N	N			Pelletier et al. (2014)

[a]Categorised as new recruit vs. experienced breeder. [b]Categorised as inexperienced vs. experienced. [c]Middle-aged group, lower boundary = minimum 4 yr of breeding experience. [d]Ages not provided

ing daylight, but younger breeders foraged more at night. However, interpretation of foraging effort is challenging in the absence of data on foraging efficiency (requiring data on energy expenditure, mass and quality of prey, etc.), since it is not clear whether increased effort might be a compensation for poor efficiency or, alternatively, if it maximises energy gain when efficiency is high. Further, such patterns are probably context dependent, with age-specific patterns in foraging effort and efficiency likely to be more pronounced during poor environmental conditions (Daunt et al. 2007a).

Considering the opposite end of the breeding lifespan, there is widespread evidence that senescence leads to a decline in breeding success in the oldest age classes (Froy et al. 2013, Nussey et al. 2013). Although the mechanisms underpinning these patterns are poorly understood, the most frequent explanation is a reduction in foraging performance with age due to physiological declines, reducing the resources that can be allocated to reproduction. Accordingly, studies have shown marked differences in the foraging performance of the oldest breeding age classes in comparison with middle-aged birds (Table 2). Catry et al. (2006) showed that old grey-headed albatrosses undertook longer trips and gained less mass than middle-aged birds. Similarly, old male wandering albatrosses undertook longer trips to remote foraging grounds and showed less foraging activity (Lecomte et al. 2010). In little penguins *Eudyptula minor*, there is spatial segregation between old and middle-aged breeders during foraging, and the oldest age classes show reduced diving effort (Zimmer et al. 2011, Pelletier et al. 2014). Differences in effort were also apparent in a study of Cory's shearwaters, where old individuals undertook fewer take-offs and landings (which are energetically expensive) and spent more time resting on the water (Catry et al. 2011).

Some studies have linked differences in activity budgets and foraging patterns between young and old birds to physiological declines (Catry et al. 2011), but others have found no physiological changes and instead interpreted this variation in terms of differences in foraging efficiency (Lecomte et al. 2010, Weimerskirch et al. 2014). However, for reasons discussed above with regard to comparisons between young and old individuals, interpretation of indices of foraging effort is not straightforward in the absence of information on energy gain. Low foraging effort in old birds may indicate poor physical fitness, resulting from physiological senescence, or may be due to high foraging efficiency, linked to experience (Catry et al. 2011, Froy et al. 2015). Furthermore, age-related declines in foraging performance are not universal; foraging behaviour of old Brünnich's guillemots *Uria lomvia* did not differ from younger adults, despite evidence for physiological senescence (Elliott et al. 2015). Age-related effects can also vary with region; in contrast to results from wandering albatrosses tracked in the Indian Ocean (Lecomte et al. 2010), there was very limited evidence for age-related variation in foraging in the same species in the southwest Atlantic, which was attributed to potential differences in oceanographic conditions (Froy et al. 2015). The ability to tease apart the effects of age from those of extrinsic conditions would be enhanced considerably by longitudinal approaches that examine within-individual changes over time (Limmer & Becker 2009, Daunt et al. 2014).

Implications for population dynamics and conservation

Despite limited evidence to date, age-specific variation in foraging and migration is likely to have important effects on individual fitness. In turn, heterogeneity in fitness among age classes will have profound consequences for population dynamics (Caswell 2001). One important mechanism underpinning these links is the interaction with extrinsic effects, whereby very young or very old individuals may be disproportionately impacted by poor environmental conditions because of lower foraging efficiency (Sydeman et al. 1991). These differences may arise from age-specific variation in susceptibility, or differences in distribution or scheduling of migration of very young or old individuals, leading to heterogeneity in environments experienced. A key factor in quantifying effects on population dynamics is the extent to which age-related variation in foraging and migration is due to ageing effects (longitudinal changes in individuals), or progressive appearance and disappearance of different phenotypes in the population (Limmer & Becker 2009, Reid et al. 2010). Long-term deployments of loggers provide opportunities to distinguish these possibilities (Daunt et al. 2014). Effects of ageing and its interaction with the environment may have important implications for conservation. Age-specific variation in migration destinations could lead to differential exposure to anthropogenic effects such as pollution or fisheries. Equally, marine protection could benefit some age classes more than others. Conservation and management initiatives could potentially target those individuals that make the highest contribution to population growth rate (Moreno 2003).

EFFECTS OF SEX

General patterns and drivers

Sexual segregation of male and female birds during foraging and migration is widespread and occurs at a range of temporal and spatial scales (Catry et al. 2005). One of the earliest studies highlighting sexual segregation in seabirds was on the wandering albatross, based on at-sea distributions of birds sexed by plumage (Weimerskirch & Jouventin 1987); this finding was later confirmed using satellite-telemetry (Prince et al. 1992, Weimerskirch et al. 1993). Sexual segregation can also involve a preference by one sex for a particular microhabitat (Table 3). In many bird families, males winter closer and return sooner to the breeding grounds than females (Cristol et al. 1999, Catry et al. 2005). An extensive, but non-exhaustive review of the recent literature on sex differences in foraging and migration since the review by Phillips et al. (2011) is provided in Table 3. Note that due to the nature of the literature search (where sex, seabirds, foraging or migration were included in the search topic in Web of Science), there may be a bias towards those studies that found positive sex differences.

Male and female seabirds may differ in scheduling of migration. Female black-browed albatrosses began migration 1 to 2 wk earlier than males and wintered further north (Phillips et al. 2005). The same pattern appears to be consistent across years in brown skuas *Stercorarius antarcticus* (Carneiro et al. 2016). In 3 species of crested penguins *Eudyptes* sp., males began migrating back to the breeding colonies earlier than females (Thiebot et al. 2014b). Recent technological advances have facilitated similar studies on smaller seabirds, which usually show a lower degree of sexual size dimorphism or are monomorphic (Table 3).

There are within-pair effects that appear to be unrelated to sex; for example if there is assortative mating of partners with similar strategies according to arrival dates. In the Scopoli's shearwater *Calonectris diomedea*, pair members do not migrate together but spend a similar number of days travelling to and from similar (but not identical) terminal nonbreeding areas (Müller et al. 2015). This was attributed to shared genes, given that pairs breeding in close proximity within the same colony (which were presumed to be more closely-related) also appeared to have similar migration strategies. In addition, paired Kerguelen shags showed some similarity in distribution and behaviour (Camprasse et al. 2017c, this Theme Section). Further, there was pair-wise segregation in wintering niche (spatial and isotopic) in the southern rockhopper penguin *Eudyptes chrysocome* but no clear sexual segregation (Thiebot et al. 2015).

The general consensus is that sexual segregation arises either from social dominance and competitive exclusion by the dominant (often larger) sex, or by habitat or niche specialization due to differences in morphology or reproductive role (Peters & Grubb 1983). Social dominance and competitive exclusion are particularly prevalent in dimorphic species where one sex has an obvious physical advantage, but there is increasing evidence for sex differences in monomorphic species as well (Lewis et al. 2002, Pinet et al. 2012, Hedd et al. 2014). A classic example of social dominance is where larger, male giant petrels *Macronectes* spp. dominate scavenging opportunities at seal and penguin carcasses on land, where interference competition clearly occurs, forcing females to primarily forage at sea (González-Solís et al. 2000). In contrast, male and female black-browed and grey-headed albatrosses are highly segregated during incubation but not during brood-guard or post-chick rearing; given that there were sex-specific differences in flight performance but no obvious role of competitive exclusion by the larger males, the seasonal segregation was attributed to niche divergence (Phillips et al. 2004).

In a recent review exploring the potential drivers or correlates of sexual segregation, stable isotope ratios rarely differed between males and females in monomorphic species, implying a link between sexual size dimorphism and segregation in diet or distribution (Phillips et al. 2011). Also, differences in $\delta^{13}C$ (reflecting carbon source) in albatrosses in the Southern Ocean suggested the underlying mechanism was related to habitat specialization, whereas in other size-dimorphic species (both male- and female-biased), sex differences were more commonly in $\delta^{15}N$ than $\delta^{13}C$, which is more consistent with size-mediated competitive exclusion or dietary specialization. Mancini et al. (2013) found no correlation between indices of sexual size dimorphism and differences in mean $\delta^{15}N$ or $\delta^{13}C$ values in males and females for 6 tropical and 5 polar seabird species, yet their review indicated that 70% of studies on dimorphic seabird species from temperate and polar regions showed some degree of trophic or spatial segregation between sexes, compared to only 20% of studies on dimorphic species in the tropics. Therefore, sexual size dimorphism appears to facilitate trophic or spatial segregation, particularly in high latitude seabirds (potentially related to more intense competition for resources during the shorter breeding season); however, even in those re-

Table 3 (this and the next page). Studies testing for sex differences in foraging and migration strategies in seabirds since 2011. Dimorphism index = (mean male mass – mean female mass)/(mean male mass + mean female mass), where positive values indicate sexual size dimorphism (SSD), and negative values indicate reverse sexual size dimorphism (RSD). Diet (trophic level)

Taxon	Mean adult mass (kg) of males (females)[a]	Dimorphism index	Wintering location	Timing of migration	Foraging location
Charadriiformes					
Brown skua *Stercorarius antarcticus*	1.765 (1.973) [17]	–0.056	N	Y	
	1.765 (1.973) [17]	–0.056			N
	1.765 (1.973) [17]	–0.056	N	Y	
Audouin's gull *Larus audouinii*	0.580 (0.492) [18]	0.082			Y*
Lesser black-backed gull *Larus fuscus*	0.941 (0.776)	0.096			Y
Black-legged kittiwake *Rissa tridactyla*	0.400 (0.400) [7]	0.000	Y	N	
Brünnich's guillemot *Uria lomvia*	0.990 (1.000) [7]	–0.005			
Atlantic puffin *Fratercula arctica*	0.480 (0.510) [7]	–0.030	Y		
Pelecaniformes					
Christmas Island frigatebird *Fregata andrewsi*	1.400 (1.550) [7]	–0.051			Y**, Y*
Australasian gannet *Morus serrator*	2.600 (2.520) [12]	0.016			N
	2.510 (2.690)	–0.035			Y
	2.600 (2.520) [12]	0.016			
Northern gannet *Morus bassanus*	2.956 (3.209)	–0.041	N		Y*
	2.930 (3.070) [7]	–0.023	N	Y	
	2.810 (3.021)	–0.036			Y
Cape gannet *Morus capensis*	2.705 (2.715) [13]	–0.002			
Masked booby *Sula dactylatra*	2.059 (2.470)	–0.091			
Imperial shag *Phalacrocorax atriceps*	2.810 (2.210)	0.120			Y
	2.285 (1.929) [14]	0.084			Y
	2.285 (1.929)	0.084			
	2.810 (2.210) [15]	0.120			
	2.285 (1.929) [14]	0.084			Y
South Georgia shag *Phalacrocorax georgianus*	2.600 (2.160)	0.092			
Kerguelen shag, *Phalacrocorax verrucosus*	2.429 (2.133)	0.065			N
European shag *Phalacrocorax aristotelis*	1.928 (1.636) [16]	0.082	N		
	1.940 (1.600) [7]	0.096			Y
	1.928 (1.636)	0.082			
Procellariiformes					
Wandering albatross *Diomedea exulans*	9.768 (7.686) [6]	0.119			
	9.768 (7.686) [6]	0.119	Y		
	9.768 (7.686) [6]	0.119			Y
	9.768 (7.686) [6]	0.119			
	9.768 (7.686) [6]	0.119	Y		Y
	9.768 (7.686) [6]	0.119	Y		
	9.768 (7.686) [6]	0.119			Y
	9.768 (7.686) [6]	0.119			Y
Black-browed albatross *Thalassarche melanophris*	3.650 (2.970)	0.103			Y
Southern giant petrel *Macronectes giganteus*	5.190 (3.940) [7]	0.137	Y		Y
Northern giant petrel *Macronectes halli*	5.000 (3.800) [7]	0.136	Y		Y
Barau's petrel *Pterodroma baraui*	0.380 (0.380)	0.000			Y*
Scopoli's shearwater *Calonectris diomedea*	0.676 (0.569) [8]	0.086	Y	Y	
	0.676 (0.569)	0.086	Y		
Cory's shearwater *Calonectris borealis*	0.880 (0.810) [9]	0.041	Y		
	0.880 (0.810) [9]	0.041	Y		
Streaked shearwater *Calonectris leucomelas*	0.549 (0.482) [10]	0.065			Y
	0.549 (0.482) [10]	0.065		Y	
Sooty shearwaters *Ardenna grisea*	0.897 (0.881)	0.009	N		Y*
Balearic shearwater *Puffinus mauretanicus*	0.509 (0.495) [11]	0.014			N
Sphenisciformes					
King penguin *Aptenodytes patagonicus*	13.981 (12.782)	0.045			
Adélie penguin *Pygoscelis adeliae*	5.350 (4.740) [1]	0.060			
Chinstrap penguin *Pygoscelis antarctica*	4.980 (4.470) [1]	0.054			
Gentoo penguin *Pygoscelis papua*	5.500 (5.060) [1]	0.042			
	5.500 (5.060) [1]	0.042			N
Southern rockhopper penguin *Eudyptes c. chrysocome*	3.917 (3.869)	0.006			Y
	3.917 (3.869) [2]	0.006	N	Y	
	3.917 (3.869) [2]	0.006			Y
Eastern rockhopper penguin *Eudyptes chrysocome filholi*	3.050 (2.980) [3]	0.012		Y	
Northern rockhopper penguin *Eudyptes chrysocome moseleyi*	2.960 (3.120) [1]	–0.026			
	2.960 (3.120) [1]	–0.026		Y	
Macaroni penguin *Eudyptes chrysolophus*	4.650 (4.890) [1]	–0.025		Y	
	4.650 (4.890) [1]	–0.025	Y	Y	
African penguin *Spheniscus demersus*	3.452 (2.996)	0.071			Y**
Magellanic penguin *Spheniscus magellanicus*	3.800 (3.000)	0.118			
	4.490 (3.709) [4]	0.095			
	4.490 (3.709) [4]	0.095			N
Humboldt penguin *Spheniscus humboldti*	4.100 (3.200)	0.123			
Little penguin *Eudyptula minor*	1.172 (1.048) [1]	0.056			N
	1.247 (1.119) [5]	0.054			

[a]Mean adult body mass was taken from the reference in the final column (if available); otherwise, it was extracted from the following sources: [1]Borboroglu & Boersma (2015), [2]Ludynia et al. (2013), [3]J.B. Thiebot pers. comm., [4]Forero et al. (2001), [5]Salton et al. (2015), [6]Tickell (1968), [7]Schreiber & Burger (2002), [8]Müller et al. (2015), [9]Ramos et al. (2009), [10]Ochi et al.

based on $\delta^{15}N$, unless indicated otherwise by '~' representing conventional diet analysis. Diet (carbon source) based on $\delta^{13}C$. BR = breeding season; NB = nonbreeding season; NB* = pre-laying. Asterisks after (Y) indicate that sex specific differences only occurred (*) during certain periods of the reproductive stage, (**) in certain years, (***) in some tissues (blood, bones or feathers)

Timing of foraging	Diving	Flight characteristics	Diet (trophic level)	Diet (carbon source)	Breeding stage	No. years in study	Reference
					NB	2	Carneiro et al. (2016)
					BR	1	Carneiro et al. (2014)
		Y			NB	3	Krietsch et al. (2017), this Theme Section
			N	N	BR	1	García-Tarrasón et al. (2015)
					BR	4	Camphuysen et al. (2015)
					NB	1	Bogdanova et al. (2011)
Y	Y*				BR	1	Elliott & Gaston (2015)
					NB	7	Fayet et al. (2016)
					BR	2	Hennicke et al. (2015)
	N	N			BR	3	Machovsky-Capuska et al. (2014)
					BR	1	Wells et al. (2016)
			Y~		BR	3	Machovsky-Capuska et al. (2016)
			Y	Y	NB, BR	3	Stauss et al. (2012)
					NB	2	Fifield et al. (2014)
	Y			Y	BR	3	Cleasby et al. (2015)
Y					BR	2	Rishworth et al. (2014b)
	Y	Y			BR	1	Sommerfeld et al. (2013)
	Y**				BR	3	Quillfeldt et al. (2011)
N	Y	N			BR	1	Quintana et al. (2011)
Y*					NB, BR	1	Harris et al. (2013)
			Y	Y	NB, BR	3	Michalik et al. (2013)
					BR	4	Harris et al. (2014b)
	Y				BR	3	Ratcliffe et al. (2013)
	N		N	N	BR	2	Camprasse et al. (2017a)
					NB	3	Grist et al. (2014)
					BR	3	Soanes et al. (2014)
	Y*				NB, BR	3	Lewis et al. (2015)
			N	Y***	NB, BR	1	Ceia et al. (2012)
					NB	1	Åkesson & Weimerskirch (2014)
					BR	1	Carravieri et al. (2014)
			Y	Y	NB, BR	1	Jaeger et al. (2014)
			Y	Y	NB, BR	24	Weimerskirch et al. (2014)
					NB	15	Weimerskirch et al. (2015)
					BR	6	Cornioley et al. (2016)
					BR	22	Jiménez et al. (2016)
					BR	1	Patrick et al. (2014)
					NB, BR	1	Thiers et al. (2014)
					NB, BR	1	Thiers et al. (2014)
		Y			NB*, BR	3	Pinet et al. (2012)
					NB	3	Müller et al. (2014)
					NB	3	Müller et al. (2015)
					NB	6	Pérez et al. (2014)
					NB	3	Pérez et al. (2016)
					NB*, BR	1	Yamamoto et al. (2011)
					NB	5	Yamamoto et al. (2014)
					NB, BR	1	Hedd et al. (2014)
					BR	4	Meier et al. (2015)
	Y		Y	N	BR	1	Le Vaillant et al. (2013)
			N	N	NB*	3	Gorman et al. (2014)
			Y	N	NB*	3	Gorman et al. (2014)
			Y	N	NB*	3	Gorman et al. (2014)
	N		Y	N	BR	1	Camprasse et al. (2017b), this Theme Section
			Y		BR	1	Ludynia et al. (2013)
			N	N	NB	1	Thiebot et al. (2015)
	Y		Y	Y	BR	3	Rosciano et al. (2016)
					NB	2	Thiebot et al. (2014b)
			Y*	Y*	BR	1	Booth & McQuaid (2013)
					NB	2	Thiebot et al. (2014b)
					NB	2	Thiebot et al. (2014b)
			N	N	NB		Thiebot et al. (2014a)
	Y				BR	2	Pichegru et al. (2013)
	Y				BR	1	Rey et al. (2013)
			N	Y***	NB	1	Silva et al. (2014)
	N		N	N	BR	3	Rosciano et al. (2016)
	Y				BR	1	Rey et al. (2013)
	N		N	N	BR	1	Pelletier et al. (2014)
			N Y~	Y**	BR	9,17	Chiaradia et al. (2016)

(2010), [11]Genovart et al. (2003), [12]G. E. Machovsky-Capuska pers. comm., [13]Rishworth et al. (2014a), [14]Harris et al. (2013), [15]Quillfeldt et al. (2011), [16]Lewis et al. (2015), [17]Phillips et al. (2002), [18]Ruiz et al. (1998)

gions, this pattern is not ubiquitous (Phillips et al. 2007, Young et al. 2010, Mancini et al. 2013) (Table 3).

Sexes may also segregate by exploiting prey at different depths, as shown in early studies on cormorants or shags *Phalacrocorax* spp., in which males made deeper and longer dives than females (Wanless et al. 1995, Kato et al. 2000). More recently, Quintana et al. (2011) used GPS and dive recorders simultaneously and found that female imperial shags *Phalacrocorax atriceps* foraged in shallow coastal waters, whereas males preferred deeper offshore waters. The authors suggested that this finding reflected the preference by each sex for foraging at depths that maximised their respective foraging efficiencies. In line with this hypothesis, sex differences in foraging behaviour and dive depths in northern gannets *Morus bassanus* appear to indicate sex-specific habitat segregation, but in this case, males foraged mostly in mixed, shallow coastal waters and females in stratified, deeper offshore waters (Lewis et al. 2002, Cleasby et al. 2015).

The sexes may also segregate temporally by undertaking foraging trips at different times of the day. In sexually dimorphic cormorants, males preferentially forage in the afternoon (Wanless et al. 1995, Kato et al. 2000, Harris et al. 2013). Links between time of day and foraging patterns are also evident in monomorphic species, including the Brünnich's guillemot *Uria lomvia*, which exhibits strong sex-specific diurnal schedules, with one sex foraging mostly at night and the other mostly at midday (Jones et al. 2002, Paredes et al. 2008, Elliott et al. 2010). Diurnal patterns of foraging in this species also resulted in spatial segregation, as males (which mostly forage at night) made shallower dives than females (in the late afternoon), presumably because males specialize on shallow prey normally found at night (Elliott & Gaston 2015).

As with effects of age, the effects of sex may be apparent only in some years. Sex differences in foraging location and diving behaviour were detected in one year in the sexually dimorphic Japanese cormorant, *Phalacrocorax capillatus*, but not in the following year when food was abundant, suggesting that segregation is more likely during intense intraspecific competition (Ishikawa & Watanuki 2002). More recently, Quillfeldt et al. (2011) showed in a multi-year study during chick rearing that larger male imperial shags dived deeper than females in some years but not others, though the mechanism was unclear.

Similarly, sex-specific foraging differences may vary with environmental conditions within years. Smaller female European shags, *Phalacrocorax aristotelis*, foraged for longer than males during strong onshore winds, but not at lower wind speeds (Lewis et al. 2015). In contrast, there was no evidence that tide or weather influenced foraging behaviour of either sex in the Brünnich's guillemot (Elliott & Gaston 2015). In other taxa, sexual segregation appears to be related more obviously to sex differences in reproductive roles (see following section).

Interactions between sex and stage of the annual cycle

Although males and females share their breeding duties to a similar extent in most seabirds, intersexual competition for food, differences in energetic or nutritional requirements, or different parental roles can lead to sexual differences in foraging behaviour during specific periods. Sex differences in stable isotope ratios are more likely during the pre-laying and later breeding periods than during the nonbreeding period (Phillips et al. 2011). Tracking studies also show that the sexes may segregate by location (Stauss et al. 2012) or time of day (Harris et al. 2013) during the breeding but not the nonbreeding season. These results imply that sex differences in foraging strategies are more likely when males and females have different reproductive roles and when potential competition and partitioning of resources between sexes are probably higher (but see Silva et al. 2014).

During the pre-laying period, males and females frequently differ in their diet or distribution, as indicated, for example, by sexual differences in isotope ratios (Phillips et al. 2011). Males (which usually perform a greater role in nest defence) often forage more locally and visit the colony more frequently, whereas females often go on a pre-laying exodus, engaging in longer foraging trips in more productive waters to meet energetic or other nutritional requirements for the clutch (Lewis et al. 2002, Yamamoto et al. 2011, Hedd et al. 2014, Quillfeldt et al. 2014, Pistorius et al. 2015). Indeed, changing energetic or nutritional requirements during the breeding cycle would explain why sex differences are apparent only at certain stages in monomorphic species such as Barau's petrel *Pterodroma baraui* (Pinet et al. 2012) or why late-incubation trips by male southern rockhopper penguins are longer, as they do all the early chick-guarding (Ludynia et al. 2013). In theory, such differences seem less likely if the male courtship feeds the female, potentially contributing substantially to clutch formation as in terns, gulls and skuas (Becker

& Ludwigs 2004), but this does not seem to be the case in the brown skua, as a higher proportion of females than males undertake a pre-laying exodus (Carneiro et al. 2016). In contrast, in some species (including gadfly petrels), males perform longer foraging trips than females, perhaps to prepare themselves for the typically-long fasting bout post-laying (Pinet et al. 2011, Rayner et al. 2012), and in the black-legged kittiwake, males are more likely than females to perform a pre-laying excursion, although the reason for this is unclear (Bogdanova et al. 2011).

Sexual differences in foraging patterns may extend into the incubation period, possibly due to the requirement for females to replenish the energy, essential nutrients or minerals spent in clutch formation. Hence, females may perform particularly long or distant foraging trips after laying (Lewis et al. 2002, Phillips et al. 2004). The emperor penguin *Aptenodytes forsteri* is an extreme example; the male incubates the egg until hatching (60–70 d), while the female forages to recover from egg formation and to gather food to feed the chick just after hatching (Williams 1995). After hatching in some penguins and alcids, males brood the chick while the females forage to provide meals for the offspring (Clarke et al. 1998, Tremblay & Cherel 2003, Paredes et al. 2006, Green et al. 2009); the reverse occurs in some terns (Becker & Ludwigs 2004).

During chick-rearing, some species show sexual differences in chick provisioning rates. Usually, these differences involve more frequent visits or larger meals from the male (Catry et al. 2005, Thaxter et al. 2009, Welcker et al. 2009), perhaps reflecting deferred costs of egg production in females or sex-specific allocation of foraging effort between parents and offspring (Monaghan et al. 1998, Thaxter et al. 2009). In Cape gannets *Morus capensis*, females undertake a greater proportion of long trips than males (Pistorius et al. 2015). In the Manx shearwater *Puffinus puffinus*, only females adopt the dual foraging strategy, whereas males perform short foraging trips and provision chicks at a higher rate (Gray & Hamer 2001). In several alcids, the role of males in provisioning chicks increases during later rearing or in the post-fledging period, when males forage closer to the colony, dive longer and deeper per day and are forced to forage at lower-quality prey patches than females (Harding et al. 2004, Thaxter et al. 2009, Elliott et al. 2010, Burke et al. 2015). Although sex differences usually decrease or disappear after the breeding period, with males and females showing similar distribution and foraging behaviour, in some species, sexual segregation in trophic niches persists year-round (Phillips et al. 2005, 2011). Males and females can differ in moulting strategies (Hunter 1984, Weimerskirch 1991), which in theory might result in different dietary needs or foraging behaviour, but this has not been investigated so far.

Interactions between sex and other factors

Sex-specific patterns of migration and foraging may involve interactions with various other intrinsic factors. For example, trip duration in the common guillemot *Uria aalge* during incubation was longer in low-quality females, i.e. those with consistently lower long-term breeding success (Lewis et al. 2006). There can also be interactions with age; older female king penguins *Aptenodytes patagonicus* conducted shorter trips, dived deeper and performed more prey pursuits during the chick rearing phase and also had higher blood $\delta^{15}N$ than younger females (Le Vaillant et al. 2013). As adults, male but not female wandering albatrosses forage progressively farther south with increasing age (Lecomte et al. 2010, Jaeger et al. 2014).

Implications for population dynamics and conservation

If sexual segregation in foraging or migration behaviour has fitness consequences and if such behaviour is heritable, there may be important evolutionary consequences (Grémillet & Charmantier 2010). However, as far as we are aware, no seabird study has determined the heritability of sex-specific foraging and migration strategies. Sexual segregation can have important implications for population dynamics and conservation if there are fitness costs associated with foraging location. One principal mechanism is that segregation leads to differing foraging efficiencies, with demographic consequences (Jaeger et al. 2014). Sex-specific variation in demographic rates could also arise from differential association with anthropogenic factors that have impacts on survival rates. Sexual segregation of wandering and other albatrosses affects the relative vulnerability of males and females to bycatch by pelagic longline fleets (Bugoni et al. 2011, Jiménez et al. 2014, Gianuca et al. 2017). Sexual segregation can also affect the relative risk of exposure to organic contaminants (Carravieri et al. 2014).

INDIVIDUAL SPECIALIZATION

Patterns of individual specialization: incidence and types

Individual specialization is generally regarded as the variation among individuals, in terms of distribution, behaviour, diet or other aspects of resource acquisition, that remains after accounting for the group effects outlined above (Bolnick et al. 2003, Dall et al. 2012). Specialization is often used to describe consistency in some aspect of the behaviour of an individual, but there is no consensus as to the minimum period over which that has to be maintained or the extent to which it may just reflect stability in the environment. The advantages and disadvantages of different approaches commonly used to detect and quantify individual specialization using conventional diet, stable isotope or tracking data are reviewed by Carneiro et al. (2017). To illustrate the diversity of research and to explore taxonomic, biogeographic and other patterns, we carried out a non-exhaustive review of studies that tested for individual specialization (Table 4). This expands on a previous review by Ceia & Ramos (2015) and includes studies examining fidelity to foraging sites, staging areas or routes during the breeding or nonbreeding seasons, and consistency in breeding-season trip characteristics, migration schedules, diving patterns and other aspects of at-sea activity, habitat use, diet or trophic level in the short or long term (Table 4).

Prior to the last decade, statistical analyses of characteristics that might reflect individual specialization were rare, although a number of studies documented consistent spatial segregation among individuals that were tracked for a sufficient length of time during the breeding (Irons 1998, Hedd et al. 2001) or nonbreeding seasons (Croxall et al. 2005). For example, in a study on grey-headed albatrosses, all were successful breeders from the same subcolony but showed diverse movement strategies during the 16 mo nonbreeding period, from largely resident in the southwest Atlantic Ocean to repeated use of the southwest Indian Ocean or more distant regions in successive winters (Croxall et al. 2005). As devices have become smaller and cheaper, many more seabird studies have shown that individuals repeatedly use the same foraging areas (i.e. show high site fidelity) in successive trips during the breeding season or in multiple nonbreeding seasons, or show consistency in departure bearing or other trip characteristics (Table 4). High nonbreeding site fidelity at a fine scale has also been determined using colour-ring resightings (Grist et al. 2014). Few studies have examined site fidelity among rather than within breeding seasons (but see Wakefield et al. 2015, Patrick & Weimerskirch 2017). During the nonbreeding season, individuals of most species tracked to date (15 of 20; see Table 4) showed a very high degree of foraging site fidelity at the regional level, with the notable exceptions of a small proportion of Cory's shearwaters, sooty shearwaters *Ardenna grisea*, long-tailed skuas *Stercorarius longicaudus* and 2 species of guillemots (Dias et al. 2011, Hedd et al. 2012, McFarlane Tranquilla et al. 2014, van Bemmelen et al. 2017, this Theme Section).

Site fidelity is usually considered to arise in seabirds either through a 'win-stay, lose-shift' strategy that is optimal if there is high spatio-temporal correlation in resource availability or through the benefit of site familiarity (Irons 1998, Wakefield et al. 2015). The incidence of site fidelity appears to be lower in the breeding than in the nonbreeding season (Table 4), but this is at least partly an issue of spatial scale and accuracy of different tracking devices: GPS loggers or satellite-transmitters for breeding birds and geolocators for nonbreeding birds. In around half of the species tracked in multiple years, site fidelity of nonbreeding birds was much lower at the mesoscale than the regional level, and there was often little or no consistency in the use of staging areas and migration routes (Table 4). Black-browed albatrosses from South Georgia were consistent in the centroid of their terminal wintering area, but not in the use of staging sites (Phillips et al. 2005); Scopoli's shearwaters showed significant repeatability in wintering region and some (but not all) aspects of migration schedule but not in the most westerly longitude reached during the return journey (Müller et al. 2014); long-tailed skuas were generally faithful to staging and wintering area and to migration routes, but as the winter progressed, a small but increasing number of individuals began to deviate from their route in previous years (van Bemmelen et al. 2017). Migration schedules (i.e. timing of departure and return to the colony and timing of major movements during the winter) were usually consistent within individuals across years, having excluded the influence of changes in breeding success or status (see Table 4). Migration timing can be affected by extrinsic factors; relative consistency in date of arrival at the colony among individual Desertas petrels *Pterodroma deserta* was attributed to potential delays because unfavourable winds increased return time from more distant regions or because birds waited for a bright moonlight night before departing (Ramirez et al. 2016).

All studies that tested for individual consistency in foraging behaviour have found evidence for this in terms of diving depth, diving or flight bout duration, proportion of daylight and darkness spent in flight, landing rate, etc. (Table 4). However, this may reflect a positive publication bias. The degree of individual variability can also change seasonally; in the imperial shag, there is an effect of photoperiod (and hence daylight available for foraging) and degree of constraint associated with breeding or moulting, on the relative consistency in the time that foraging begins and ends each day (Harris et al. 2013, 2014b). Results from conventional stomach contents or stable isotope ratios indicate significant consistency within individuals in many species in habitat use, prey type or trophic level in the short or long term (days to weeks, between the breeding and nonbreeding seasons or annual); however, there were exceptions, particularly among the albatrosses and petrels (Table 4).

Drivers of individual specialization: influence of species and sex

Individual specialization in some form has been recorded in all orders of seabirds (Sphenisciformes, Procellariiformes, Pelecaniformes and Charadriiformes) but only half of the families (Spheniscidae, Diomedeidae, Procellariidae, Sulidae, Phlacrocoracidae, Stercorariidae and Laridae, but not Pelecanoididae, Hydrobatidae, Fregatidae, Phaethontidae, Sternidae and Rhynchopidae) (Table 4). This likely reflects a research bias, with fewer studies on tropical seabirds and less tracking of smaller species because of the greater impacts of devices on these birds. The correspondence between the presence or absence of individual specialization and phylogeny or region is therefore unclear; nevertheless, all 10 studies to date that tested for individual specialization in diverse aspects of movement and foraging behaviour of cormorants and shags have found evidence for its existence, suggesting that it is the dominant pattern in those taxa (Table 4).

Several studies have compared the degree of site fidelity or behavioural consistency between males and females, but results do not show a clear pattern. Long-term consistency in habitat use was greater in male than in female wandering albatrosses, possibly because females shift distribution to the north to reduce competition with males in the nonbreeding period (Ceia et al. 2012). Female imperial shags were less variable in the timing of foraging and other trip characteristics, attributed to the lower costs of foraging in males and hence their greater discretionary time for accommodating the female, which typically takes the first foraging shift each day (Harris et al. 2013, 2014b). In Kerguelen shags *Phalacrocorax verrucosus*, males were less specialized in diving behaviour than females (Camprasse et al. 2017a). Similarly, males showed more variability in dive depths in South Georgia shags *Phalacrocorax georgianus*, possibly because maximum dive depth is more closely correlated with body mass in females (Ratcliffe et al. 2013). Female Audouin's gulls *Larus audouinii* foraged at sea throughout the week, whereas males switched from foraging at sea during weekdays to inland coastal habitats (rice fields) on weekends, when fisheries discards were unavailable (García-Tarrasón et al. 2015). In other studies, there were no differences in behavioural consistency or wintering site fidelity between sexes (Grist et al. 2014, Potier et al. 2015), or there were sex differences in consistency, but the direction depended on the parameter (Müller et al. 2014).

Extrinsic explanations for individual specialization: influence of prey predictability

Individual specialization appears to be widespread in cormorants and shags (Table 4). This seems likely to be related to their exploitation of benthic prey, which may be constrained in terms of seabed habitat. Such habitats contain numerous static features, enabling foraging birds to memorize topographic cues to improve encounter rate. Differing degrees of spatial and temporal predictability of resources might also explain relative fidelity to foraging sites in more pelagic seabirds, as particular areas (shelf, shelf breaks, fronts, etc.) reliably hold more prey resources, and individuals return there in successive trips. Indeed, this was the suggested explanation for consistent differences in trip bearings and repeatability in travel distances of individual northern gannets only at the Bass Rock and not Great Saltee, UK, on the basis that predictability of resources was higher in the North Sea than in the Irish Sea (Hamer et al. 2001). However, specialization does not always relate to resource predictability; black-browed albatross, shy albatross *Thalassarche cauta* and razorbill *Alca torda* were not consistent in site or habitat use although they all fed in neritic waters (Hedd et al. 2001, Granadeiro et al. 2014, Shoji et al. 2016). In addition, although it is intuitive that specialization would be less likely in tropical waters, given the

Table 4 (this and the next 3 pages). Evidence for significant individual specialization in distribution, movements, activity or diet of seabirds. √: significant effect; (√): some evidence but with exceptions; X: study tested explicitly for specialization but found no evidence; W: within breeding season; B: between breeding seasons; N: nonbreeding site; R/S: route or staging area; Dep: at departure; Dur: during; Ret: at return; ST: short-term (days to weeks); LT: between seasons or annual

Species	Breeding colony	Foraging site fidelity within or between breeding seasons	Foraging trip bearing or distance (breeding season)	Fidelity to nonbreeding site, route or staging area[a]
King penguin *Aptenodytes patagonicus*	Falklands	W - X	√	
Macaroni penguin *Eudyptes chrysolophus*	South Georgia			
Southern rockhopper penguin *Eudyptes c. chrysocome*	Falklands			
Adélie penguin *Pygoscelis adeliae*	Syowa Station, Antarctica	W - (√)		
Little penguin *Eudyptula minor*	Penguin Island, Australia			
Yellow-eyed penguin *Megadyptes antipodes*	Oamaru, New Zealand	W - √		
Black-browed albatross *Thalassarche melanophris*	South Georgia			N - √, R/S - X
	Falklands			
	Kerguelen	W - (√), B - (√)	√	
Grey-headed albatross *Thalassarche chrysostoma*	South Georgia			N - √
Shy albatross *Thalassarche cauta*	Tasmania	W - X, B - X	√	
Light-mantled albatross *Phoebetria palpebrata*	South Georgia			
Wandering albatross *Diomedea exulans*	South Georgia			
	Crozet			N - √
White-chinned petrel *Procellaria aequinoctialis*	South Georgia			
Yelkouan shearwater *Puffinus yelkouan*	Malta			N - √
Short-tailed shearwater *Ardenna tenuirostris*	Tasmania			N - √
Sooty shearwater *Ardenna grisea*	Kidney Island (Falklands)			N - (√), R/S - (√)
Streaked shearwater *Calonectris leucomelas*	Sangan, Mikura, Awa Islands, Japan			N - √, R/S - √
Cory's shearwater *Calonectris borealis*	Selvagem Grande (Madeira)			N - (√), R/S - X
	Berlenga (Portugal)			
	Canary Islands	W - √		
Scopoli's shearwater *Calonectris diomedea*	Sicily (Italy)			N - √, R/S - X
Desertas petrel *Pterodroma deserta*	Madeira			N - √
Thin-billed prion *Pachyptila belcheri*	New Island, Falklands			
Broad-billed prion *Pachyptila vittata*	Rangatira, Chatham Islands			
Northern gannet *Morus bassanus*	Bass Rock (UK)	W - √, B - √	√	
	Great Saltee (UK)	W - X	X	
	Grassholm (UK) and Brittany (France)	W - √	√	
	Alderney	W - X	√	
	Various colonies, Canada			N - √
	North Norway	W - X	(√)	

Consistent migration schedule[b]	Consistent activity or diving pattern	Consistent habitat use[c] in short- or long-term	Consistent diet or trophic level[d] in short- or long-term	Reference
				Baylis et al. (2015)
	√	LT - √		Green et al. (2005), Horswill et al. (2016)
		LT - √	LT - √	Dehnhard et al. (2016)
				Watanuki et al. (2003)
	√			Ropert-Coudert et al. (2003)
				Mattern et al. (2007)
Dur - √, Ret - √	√			Phillips et al. (2005), Mackley et al. (2010)
		ST - X ST - √	ST - X	Granadeiro et al. (2014) Patrick & Weimerskirch (2014b, 2017)
	√			Croxall et al. (2005), Mackley et al. (2010)
				Hedd et al. (2001)
	√			Mackley et al. (2010)
	√	ST - √, LT - √	ST - √, LT - X	Mackley et al. (2010), Ceia et al. (2012) Weimerskirch et al. (2015)
	√			Mackley et al. (2011)
Dep - √, Dur - √, Ret - √				Raine et al. (2013)
				Yamamoto et al. (2015)
Dep - (√), Dur - (√)				Hedd et al. (2012)
Dep - √, Dur - √				Yamamoto et al. (2014)
Dep - √, Dur - √, Ret - √				Dias et al. (2011), Dias et al. (2013)
		ST - (√)	ST - (√)	Ceia et al. (2014) Navarro & González-Solís (2009)
Dep - X, Dur - √, Ret - X				Müller et al. (2014)
Dep - √, Ret - √		LT - √	LT - √	Ramirez et al. (2016)
		ST - √, LT - X	ST - √, LT - X	Quillfeldt et al. (2008)
		LT - X	LT - X	Grecian et al. (2016)
	√	ST- √, LT - √	ST - √, LT- √	Hamer et al. (2001, 2007), Wakefield et al. (2015)
	√	ST - √	ST - √	Hamer et al. (2001) Votier et al. (2010), Patrick et al. (2014)
Dur - √, Ret - √				Soanes et al. (2013) Fifield et al. (2014) Pettex et al. (2012)

(table continued on next 2 pages)

(Table 4 continued)

Species	Breeding colony	Foraging site fidelity within or between breeding seasons	Foraging trip bearing or distance (breeding season)	Fidelity to nonbreeding site, route or staging area[a]
Great cormorant *Phalacrocorax carbo*	Chausey Islands, France	W - √, B - √		
European shag *Phalacrocorax aristotelis*	Isle of May (UK)			
Imperial shag *Phalacrocorax atriceps*	Argentina	W - √	√	
South Georgia shag *Phalacrorax georgianus*	South Georgia			
Kerguelen shag *Phalacrocorax verrucosus*	Kerguelen	W - √	√	
Crozet shags *Phalacrocorax melanogenis*	Possession Island, Crozet			
King cormorant *Phalacrocorax purpurascens*	Macquarie Island			
Pelagic cormorant *Phalacrocorax pelagicus*	Gulf of Alaska	W - √		
Double-crested Cormorant *Phalacrocorax auritus*	Oneida Lake, New York, USA	W - √		
Japanese cormorants *Phalacrocorax capillatus*	Teuri Island, Japan	W - √	√	
Razorbill *Alca torda*	Skomer (UK)	W - X	X	
Atlantic puffin *Fratercula arctica*	Skomer			N - √, R/S - √
Great skua *Stercorarius skua*	Bjørnøya Shetland, UK	W - √		N - √
Brown skua *Stercorarius lonnbergi*	South Georgia South Shetland Islands			N - √
South polar skua *Stercorarius maccormicki*	King George Island			N - √
Long-tailed skua *Stercorarius longicaudus*	Sweden, Svalbard, and Greenland			N - (√), R/S - (√)
Lesser black-backed gull *Larus fuscus*	North Norway			N - √
Yellow-legged gull *Larus michahellis*	Gulf of Cadiz, Spain			
Dolphin gull *Leucophaeus scoresbii*	Falkland Islands	W - √		
Black-legged Kittiwake *Rissa tridactyla*	Prince William Sound, Alaska Pribilof Islands	W - √		 N - (√), R/S - (√)
Pigeon guillemot *Cepphus columba*	Prince William Sound, Alaska			
Brünnich's guillemot *Uria lomvia*	Various colonies, Canada Nunavut, Canada			N - (√)
Common guillemot *Uria aalge*	Various colonies, Canada Newfoundland, Canada	W - √	√	N - (√)

[a]Studies only included if 2 or more individuals tracked in multiple years. [b]Where possible, studies were excluded that did not control for differences in breeding success between years. [c]Includes results from tracking and stable isotope studies. [d]Includes conventional diet and stable isotope studies

greater variability and patchiness of resources (Weimerskirch 2007), streaked shearwaters *Calonectris leucomelas,* which migrate to tropical waters, showed a high degree of fidelity to nonbreeding destination and migration route (Yamamoto et al. 2014). Availability and predictability can also vary over time in the same habitats, which might partly explain why the degree of consistency in diet or isotopic niche in the same species can depend on breeding stage and year (Ceia et al. 2014).

Consistent migration schedule[b]	Consistent activity or diving pattern	Consistent habitat use[c] in short- or long-term	Consistent diet or trophic level[d] in short- or long-term	Reference
	√			Grémillet et al. (1999), Potier et al. (2015)
	√			Daunt et al. (2014)
	√			Harris et al. (2013, 2014b)
	√	LT - √	LT - √	Bearhop et al. (2006), Ratcliffe et al. (2013)
	√	ST - √, LT - √	ST - √, LT - √	Bearhop et al. (2006), Camprasse et al. (2017a)
	√			Cook et al. (2006)
	√			Kato et al. (2000)
	√			Kotzerka et al. (2011)
				Coleman et al. (2005)
	√			Ishikawa & Watanuki (2002)
				Shoji et al. (2016)
Dur - √				Guilford et al. (2011), Fayet et al. (2016)
				Magnusdottir et al. (2012)
			ST - √, LT - √	Votier et al. (2004)
		LT - √	LT - √	Phillips et al. (2007)
Dep - √, Ret - √	√			Krietsch et al. (2017), this Theme Section
				Kopp et al. (2011)
				van Bemmelen et al. (2017), this Theme Section
				Helberg et al. (2009)
		√		Navarro et al. (2017), this Theme Section
			ST - √	Masello et al. (2013)
				Irons (1998)
				Orben et al. (2015b)
			LT - √	Golet et al. (2000)
Dep - X, Ret - X	√			McFarlane Tranquilla et al. (2014)
	√	ST - √	ST - √, LT - √	Woo et al. (2008), Elliott et al. (2009)
Dep - (√), Ret - √	√			McFarlane Tranquilla et al. (2014)
				Regular et al. (2013)

Development of individual specialization: the role of learning

Individual specialization is expected to offer a selective advantage where resources are to some extent predictable; under these circumstances, birds can increase foraging efficiency by reducing search times or develop proficiency in locating or handling particular types of prey. Specialization, particularly site fidelity, likely develops largely from experience gained

(learned) when seabirds are immature. During these formative years, individuals show high variability in dispersal and movement patterns (Thiers et al. 2014, de Grissac et al. 2016), in which the roles of genetics and experience are not well understood. Whether individual wandering albatrosses are partial or full migrants does not appear to be heritable (Weimerskirch et al. 2015). However, because fledgling seabirds migrate for the first time without parents, initial dispersal direction — and potentially the distance travelled — may be heritable as in other birds (Piersma et al. 2005).

Although intrinsic factors will also play a role, in the absence of a central-place foraging constraint, the subsequent timing of movements and areas visited by immatures is probably dictated to a considerable extent by local conditions (including weather) and the availability, patchiness and predictability of prey (Mueller & Fagan 2008). Individual migration pattern probably becomes fixed according to experience (Guilford et al. 2011, Péron & Grémillet 2013, de Grissac et al. 2016). There is no effect of age *per se* on the nonbreeding strategy in the wandering albatross (Weimerskirch et al. 2015) nor on the likelihood of an adult shifting its winter destination in the Cory's shearwater (Dias et al. 2011). Indeed, Cory's shearwaters may switch back and forth between different regions (Dias et al. 2013), and long-tailed skuas may switch between different routes in successive migrations (van Bemmelen et al. 2017), indicating that these changes are not the result of accidental displacement by severe weather conditions. Hence, knowledge of the previous experience of the individual is key to understanding the navigation process, and the development of individual specialization in movements in general.

Learning may also be responsible for development of individual specializations in diving behaviour, particularly as benthic feeders such as shags and cormorants would benefit from local knowledge of bottom topography and currents (Table 4). Learning could also explain consistency in at-sea activity patterns (including in flights and landings), trophic level or diet, even in pelagic species, as individuals may specialize in locating or handling particular types of prey (Table 4). Indeed, learning seems the likeliest explanation for dietary specializations in highly opportunistic species with diverse diets, such as great skua *Stercorarius skua*, brown skua and dolphin gull *Leucophaeus scoresbii*, which presumably need to develop particular skills to successfully pursue different foraging modes, whether that is kleptoparasitism, predation of selected species or scavenging, etc. (Votier et al. 2004, Phillips et al. 2007, Masello et al. 2013).

Implications of individual specialization

Links to physiology and life-history

Many studies have related differences between individuals in distribution, timing, foraging success, etc. to body condition, past experience or future breeding performance (Bogdanova et al. 2011, Orben et al. 2015a). By comparison, only a few studies have examined the physiological correlates of specialization or the energetic or life-history consequences. Specialization should in theory be advantageous if an individual has fixed on a particular strategy that is more profitable than the alternatives. Positive evidence for an advantage of specialization is particularly apparent among predatory seabirds. Specialist western gulls *Larus occidentalis* that maintained feeding territories within colonies of other seabirds had higher reproductive success and similar or higher survival rates compared to non-specialists (Spear 1993). Pairs of slaty-backed gulls *Larus schistisagus* that delivered more depredated seabird chicks raised more fledglings, and their chicks grew faster than those of pairs that mainly delivered fish, possibly because of the differences in energy value of the meals (Watanuki 1992). Individual specialization has also been linked to potential fitness advantages in other seabirds. There were significant relationships between repeatability in some dive characteristics of great cormorants *Phalacrocorax carbo* and foraging efficiency (Potier et al. 2015). In the black-browed albatross, foraging trip characteristics were less variable in successful than unsuccessful male breeders and in females that were more faithful to foraging sites but not necessarily to habitat (water depth) had higher reproductive success (Patrick & Weimerskirch 2014a, 2017). Pairs of pigeon guillemots *Cepphus columba* that were dietary specialists fledged more chicks than the diet generalists, apparently because they delivered larger individual prey items (Golet et al. 2000).

Individual specialization has been linked to carry-over effects in a number of studies. Individual European shags showed consistent differences in daily foraging times during winter, and the shorter foraging times were associated with earlier and more successful breeding, demonstrating a clear carry-over effect (Daunt et al. 2014). In this context, it is important to note that carry-over effects may be evident in only a proportion of colonies (Bogdanova et al. 2017); it is also often hard to exclude the possibility that a cross-seasonal correlation is unrelated to specialization and instead due to stable within-individual performance, i.e.

consistently good or poor performance or decision-making year-round (Harrison et al. 2011). The mechanisms underlying carry-over effects are not always clear, but it seems that stress (reflected in feather corticosterone levels) affects energy or nutrient acquisition and hence physiological condition, which has impacts on behaviour and performance in the subsequent season (Young et al. 2017, this Theme Section).

Intuitively, consequences of individual specializations might be most obvious when examining effects of migration distance, as those individuals that travel the furthest incur greater energy or time costs, reducing the time available for feeding and resting en route or delaying the return to the colony. Late return has repercussions for nest defence, mating opportunities or re-establishment of the pair bonds and, ultimately, timing of laying, which is typically closely correlated with breeding performance. Yet, 2 studies did not find evidence of a substantial energetic advantage for individuals that remained closer to the colony, having accounted for flight time to and within alternative wintering areas and for thermoregulatory costs associated with resting on the water (Garthe et al. 2012, Fort et al. 2013). Similarly, Ramirez et al. (2016) did not detect differences in the level of individual repeatability in at-sea activity patterns of Desertas petrels that migrated to different wintering areas. In theory, the choice of a short- or long-distance migration strategy may be neutral, reflect individual optima or vary in terms of advantages or disadvantages for survival or reproduction depending on the year. If so, individual specialization in the form of high nonbreeding-site fidelity may not affect subsequent body condition, survival or fitness unless there is a major deterioration in the environment.

Various studies have not detected any convincing selective advantage of individual specialization. Northern gannets that associated consistently with fishing vessels were not in better body condition than those which avoided vessels (Patrick et al. 2015); short- and long-term consistency in trophic level or carbon source was not related to body mass index in wandering albatrosses (Ceia et al. 2012); there were no effects of foraging area or site fidelity on chick feeding frequency or meal mass in Adélie penguins *Pygoscelis adeliae* (Watanuki et al. 2003) nor on breeding success in European shags (Daunt et al. 2014); although Brünnich's guillemots that were generalists tended to deliver slightly more energy per day, specialists and generalists did not differ in any other aspect of fitness (Woo et al. 2008); great skuas that were bird specialists consistently laid earlier, had larger clutch volumes and improved chick condition but did not have higher breeding success or survival than specialist fish predators (Votier et al. 2004); lastly, consistency within or among years in trip or dive characteristics did not influence body condition in northern gannets (Wakefield et al. 2015). The lack of a clear fitness benefit in many cases may be related to changes over time in the predictability of resources, which could fluctuate within and between breeding seasons. Specialists may be at an advantage when predictability is high in certain areas, whereas generalists likely benefit when resource availability is less predictable and more heterogeneous.

Links to population dynamics and conservation

An understanding of variation both among and within individuals allows the characterization of populations and has implications for their resilience in the face of environmental change (Nussey et al. 2007). Unless there is time for selection to act, populations that lack variability and individuals that lack plasticity in movements and foraging behaviour are

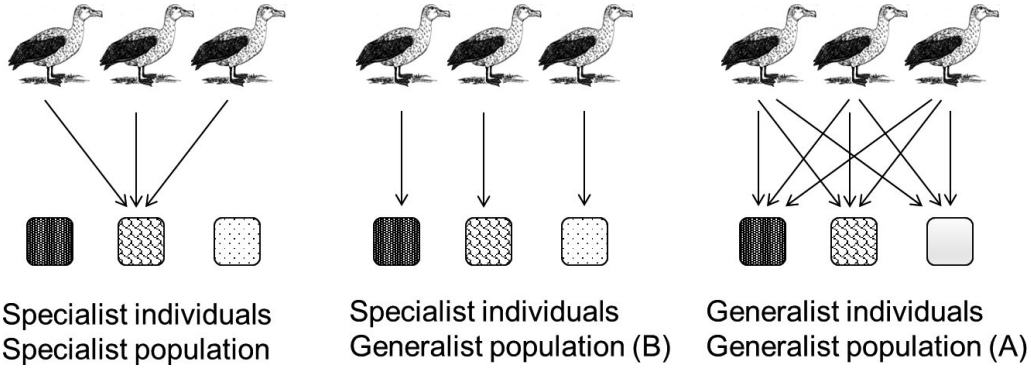

Fig. 1. Use of different resources or habitats (represented by different shading) for more or less generalist or specialist populations

likely to be at a considerable disadvantage. This is illustrated by the schematic based on Bolnick et al. (2003), which illustrates different hypothetical situations of resource (or habitat) use in Fig. 1: (1) generalist individuals from a generalist population all target multiple alternative resources (type A); (2) specialist individuals from a generalist population consistently target one of multiple alternative resources (type B); and (3) specialist individuals from a specialist population all consistently target the same resource. The implications are that in the absence of a change in behaviour, the loss or deterioration of one resource or habitat would be catastrophic for the specialist population (and for the specialists in the generalist population that targeted that resource) but of less consequence for the generalists, depending on density-dependent competition for the resources that remain. This can have implications in the design of marine protected areas, since population-based approaches may not identify important areas used by a relatively low proportion of specialized individuals, or these areas may not be prioritized for management. However, those areas, and the specialists that use them, may buffer population-level impacts of a deterioration in habitats used by the majority of birds. The same principle applies to a localized increase in pollutants, competition with fisheries or fisheries bycatch, etc. Indeed, many threats show extensive spatial heterogeneity, such as fisheries bycatch risk (Phillips et al. 2009a, Thiers et al. 2014) and exposure to pollutants, including plastics, mercury, persistent organic pollutants and hydrocarbons (Young et al. 2009, Montevecchi et al. 2012, Leat et al. 2013, Tartu et al. 2013).

The importance of assessing the extent and duration of specialization can be illustrated by considering exposure to fisheries. In the Falklands, there were significant differences between 2 study colonies of black-browed albatrosses in the degree of bird association with vessels, despite equal distances to fishing areas (Granadeiro et al. 2011, 2014). Those studies showed that a minority of individuals repeatedly followed vessels, suggesting they specialized in the short-term on fisheries waste, but tracking in a subsequent year and stable isotope analyses suggested that any fisheries specialism did not persist. In contrast, individual northern gannets did show specialization in following vessels or feeding on fisheries waste (Patrick et al. 2015). Hence, in the absence of any mitigation, fisheries bycatch represents a constant risk to black-browed albatrosses that would be maintained indefinitely if a proportion of the generalist population is attracted to vessels at random, but a particular risk for a specific group of specialist northern gannets that might be removed and not replaced. The demographic implications of these and other threats depends on the diversity of strategies (from specialist to generalist) in the population, the probability of individuals encountering adverse conditions, the degree of individual plasticity and the heterogeneity in vital rates associated with among-individual specialization. Seabirds are clearly highly adaptable in response to environmental pertubation, and some specializations can be relatively short-lived (Wakefield et al. 2015). Movement of individuals during the breeding and nonbreeding seasons are clearly flexible, but other aspects of behaviour (such as departure bearings of fledglings) or timing of some events may be innate, possibly responding to magnetic cues or stimuli that are highly predictable, such as photoperiod; however, even then, there may be some capacity for fine-tuning in response to environmental factors (Helm et al. 2013).

CONCLUSIONS

As this review has shown, many intrinsic factors (including stage of the annual cycle, breeding status, age and sex) drive individual differences in movement patterns and behaviour of seabirds. Understanding the nature, drivers and consequences of this variation is revealing in terms of ecology and life-histories and determines the response of individuals, populations and species to environmental changes, including anthropogenic threats. In addition, the effects of intrinsic factors and their interactions with each other and with the environment need to be considered in sampling design and analyses, and before drawing conclusions about underlying processes and mechanisms. They also need to be taken into account when evaluating evidence for individual specialization and its causes and consequences. Effects of factors such as sex, stage, age, as well as individual specializations are common in terms of distribution, habitat use, diving, diet and other components of foraging strategies at sea, but their roles and extents are highly variable. Site fidelity is scale-dependent for migrants, greater at the regional level than in the use of staging areas and routes, and can be low during the breeding season (Table 4). Timing of movements during the nonbreeding period is often consistent, but with some flexibility in response to local conditions. As might be expected, seabirds retain the flexibility to respond to local environmental conditions or cues and intrinsic factors (body condition, physiological constraints, etc.).

There is much scope for more studies on the timescale or periods in which effects of sex, age and specialization are apparent (from days to years) and the drivers underpinning these factors (resource availability and predictability, density-dependent competition, intrinsic characteristics, learning). Adults clearly use memory (Regular et al. 2013) to guide subsequent decisions; under what conditions (i.e. changes in resource availability or habitat suitability) they might re-enter an exploratory phase as adults and refine their movement and foraging strategies is unknown. Although the papers in this Theme Section have increased our understanding of the implications of individual variation and specialization, there are still many gaps in our knowledge. With regard to individual specialization in particular, we would recommend research on the circumstances in which it offers a selective advantage, the degree of genetic or cultural transmission, the level of plasticity in response to the environment, the energetic and other physiological consequences and effects (immediate or carry-over) on survival and reproduction. This is particularly important in a rapidly changing world, as the degree of plasticity of individuals affects the capacity of populations to respond to changes in conditions.

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